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Podocnemis venezuelensis, a new fossil pelomedusid (Testudines, Pleurodira) from the Pliocene of Venezuela and a review of the history of *Podocnemis* in South America

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ABSTRACT. *Podocnemis venezuelensis*, a new species of pelomedusid turtle from the mid-Pliocene (Huayquerian) of Venezuela is described. Present evidence is insufficient for determining whether it was a marine or a fresh water form. Previously described South American fossil species that have been attributed to *Podocnemis* are discussed. Of these, only two — *P. bassleri* and *P. elegans* — are surely referable to this genus. It is concluded that the fossil record of *Podocnemis* is not yet adequate for reconstructing its evolutionary history on this continent.

RESUMEN. Se describe una nueva especie de tortuga pelomedusida del Plioceno medio (Huayqueriense) de Venezuela, *Podocnemis venezuelensis*. Las presentes pruebas son insuficientes para determinar si fué de aguas marinas o de agua dulce. Se discuten las especies suramericanas fósiles que han sido atribuidas a *Podocnemis*. De estas, solo dos — *P. bassleri* y *P. elegans* — son valederas. Se concluye que el registro fósil de este genero no es aún adecuado para la reconstrucción de su historia evolutiva en este continente.

INTRODUCTION

Only one species of fossil turtle, *Podocnemis geologorum* (Simpson, 1943), has ever been formally described from Venezuela. Other occurrences of Venezuelan fossil chelonians have,

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however, occasionally been mentioned: Swinton (1928) referred three specimens "too fragmentary for specific determination," of Pliocene or Pleistocene age (Van Frank, 1957: 22n), to "*Testudo* sp."; and Royo y Gomez (1960) published a faunal list of fossil vertebrates discovered in what is now known as the upper member of the Urumaco Formation, that included ". . . varios caparazones completos . . . de tortugas palustres (*Podocnemys*)" which he believed to be of mid-Miocene age. Unfortunately, the untimely death of Royo y Gomez in 1961 prevented his describing any of this material. The specimens, however, are preserved in the collections of the Universidad Central de Venezuela in Caracas. Except for one report on rodent remains (Pascual and Diaz de Gamero, 1969) and another on a new gavial (Sill, 1970), nothing has been published on them. The fossil turtles are described here.

Abbreviations used in this paper are:

AMNH — the American Museum of Natural History, New York

MCN — Museo de Ciencias Naturales, Caracas

VF — Laboratorio de Paleontologia, Escuela de Geologia de la Facultad de Ingeniera de la Universidad Central de Venezuela (Caracas).

CLASSIFICATION AND DESCRIPTION

Order **Testudines**

Suborder **Pleurodira**

Family **Pelomedusidae**

Genus **Podocnemis**

A cautionary word is appropriate concerning the attribution of fossil material to *Podocnemis*. Most extinct species of this genus are known solely from shell material. However, at least one other fossil genus, *Bothremys*, has a shell that is virtually indistinguishable from that of *Podocnemis*. In fact, two purported species of *Podocnemis*, *P. barberi* (Schmidt, 1940) and *P. alabamiae* (Zangerl, 1948), were originally described on the basis of shell material that, upon the later discovery of associated skull material, has subsequently been referred to the genus *Bothremys* (Gaffney and Zangerl, 1968). Conceivably, therefore, when skulls become known for some of the fossil species now referred to *Podocnemis*

on the basis of their shells, it may be necessary to transfer them elsewhere. The new species described in this paper is placed in *Podocnemis* with this caveat.

Podocnemis venezuelensis sp. nov.

(Figures 1-3 and Plates I-V)

Type. VF 1176, a complete carapace, slightly flattened, including much of the axial buttresses and the pelves, the latter badly damaged. Also, VF 1173, a fairly complete but badly fractured plastron lacking only the entoplastron and epiplastra. Although bearing a different number, the plastron is of an appropriate size and state of preservation so that we believe it highly probable that both of these shell elements are from the same individual (see Plate IV). Unfortunately, none of Royo y Gomez's notes contain information bearing on this point.

Hypodigm. The type, and VF 1174, a plastron lacking the posterior lobe; VF 1175, the anterior one-third of a carapace; VF 1177, a complete carapace and plastron, considerably flattened, of a relatively small individual; VF 1177a, a nearly complete carapace and plastron of the largest individual in the sample, lacking only the pygal and posterior portions of both eleventh peripherals; VF 1177b, the left epiplastron, hyoplastron, and left one-half of the entoplastron, plus several pleurals attached to part of the bridge, probably all belonging to the same individual; VF 1059, the distal end of a right humerus.

Horizon and locality. The "capa de huesos" or "capa de tortugas" (Pascual and Díaz de Gamero, 1969: 373 and map) of the upper member of the Urumaco Formation, probably of mid-Pliocene (Huayquerian) age, north of Campo El Mamón, state of Falcón, Venezuela.

The Uramaco Formation is divided into three members, designated as lower, middle, and upper. The lower and middle members are largely, if not entirely, of marine origin while the upper member apparently includes both littoral or deltaic as well as more strictly terrestrial facies. Marine molluscs from the middle member were the basis for the original age determination of mid-Miocene for this formation. This was subsequently revised to late Miocene. However, the recent study of Pascual and Díaz de Gamero (1969: 379) indicates that at least the "bone bed" of the uppermost part of the upper member is probably of middle

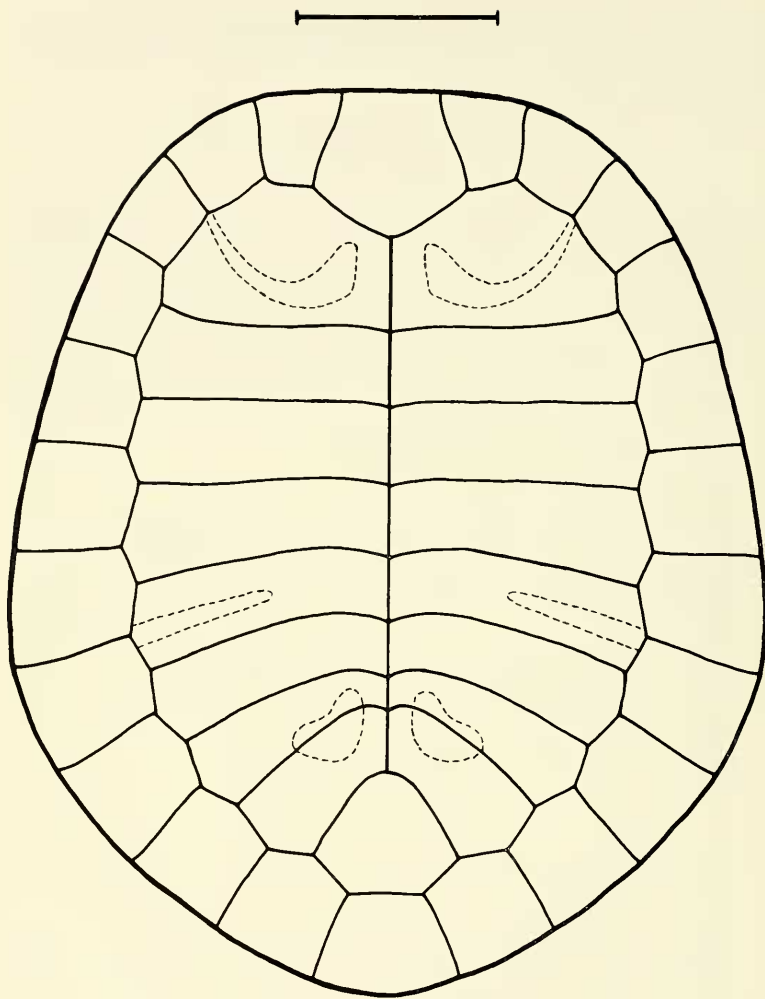


Figure. 1 Reconstruction of the shell of *Podocnemis venezuelensis* (dorsal view). The scale represents a length of 15 centimeters. The positions of the axial and inguinal buttresses as well as of the iliac scars of the pelvis on the visceral surface of the carapace are indicated by the broken lines.

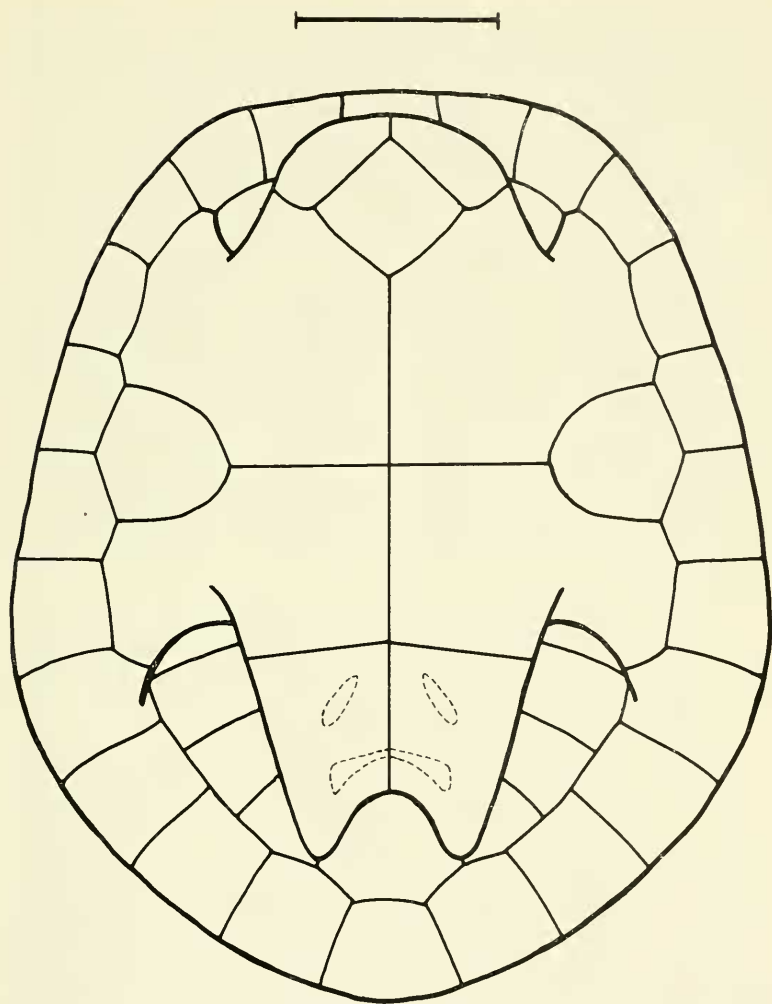


Figure 2. Reconstruction of the shell of *Podocnemis venezuelensis* (ventral view). Same scale as in Fig. 1. The positions of the pelvic scars on the visceral surface of the plastron are indicated by the broken lines.

Pliocene (Huayquerian) age. Palynological evidence appears to confirm this date (A. E. González Guzmán, personal communication). It is possible that there may be a temporal hiatus between the middle and upper members of the Urumaco Formation that cannot be detected structurally; an explanation of this nature would account for the different age determinations of the middle and upper members of the Urumaco Formation.

Diagnosis. Differs from all other species of *Podocnemis* in totally lacking neural bones.

Description. It is unfortunate that a gypsiferous encrustation on the external surfaces of all of the specimens obscures most of the bone sutures and virtually all scute sulci. Nevertheless, an essentially complete osteological description of the shell is possible from examination of the visceral surfaces of the type and some other, less complete specimens. Although the outlines of any particular bone may differ somewhat from the external to the internal surface of the shell, as Dacqué (1912: 290 and fig. 7) has demonstrated, it is nonetheless possible to make a reasonable reconstruction of the shell of a typical representative of the species (see Figures 1 and 2).

Adult specimens of *Podocnemis venezuelensis* attained a rather large size. The three complete carapaces in our sample range from approximately 46 to 67 centimeters¹ in length. Of the eight living species of *Podocnemis*, only two, *P. expansa* and *P. unifilis*, are reported to reach a larger maximum size.

In cross section, the arch of the carapace is very flat; in outline it is somewhat oval and greatly expanded posteriorly. The external surface of the carapace is completely smooth. No significant indentation occurs in the nuchal region. Well-developed axial and inguinal buttresses unite the carapace to the plastron. The plastron itself is essentially flat and of nearly uniform thickness throughout.

The outstanding feature of the carapace, and indeed the character permitting definition of a new species, is the complete absence of neural bones. Otherwise, the carapace is typical of other South American representatives of the genus. The nuchal bone is roughly pentagonal and slightly broader than long in its maximum dimensions; its postero-lateral borders are bowed outwards

¹ The larger number represents the estimated total length of VF 1177a; its actual midline length as preserved is 60.1 centimeters.

slightly. There is no indentation at the midline of the anterior margin. The eight pairs of pleurals meet in the midline. As in all pelomedusids, there are eleven pairs of peripherals. The pygal is trapezoidal and the suprapygal is roughly subtriangular. Butresses of the axial and inguinal notches are attached to the undersides of the first and fifth pleurals respectively. The iliac scars of the pelvis are situated on the visceral surfaces of the seventh and eighth pair of pleurals.

Of the three elements of the plastron, the bridge is the longest while the anterior lobe is the shortest. The anterior plastral lobe is U-shaped and does not extend beyond the anterior lip of the carapace. The lateral margins of the posterior lobe are straight rather than curved and are inclined medially so that the posterior lobe becomes narrower toward the rear. The entoplastron is diamond-shaped and has a slight U-shaped ridge with the open end facing anteriorly on its visceral surface; this is presumably for the attachment of neck muscles. At the midline junction of the epiplastra there is a pronounced protuberance on the visceral side. The mesoplastra are subrounded to hexagonal elements situated

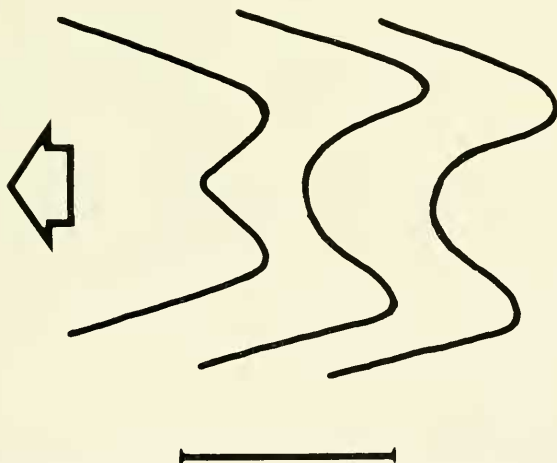


Figure 3. The shape of the anal notch in three specimens of *Podocnemis venezuelensis* (from left to right, VF 1177, VF 1173 and VF 1177a). The arrow points toward the anterior end of the shell. The scale represents a length of 10 centimeters.

laterally at the base of the bridge. (These can best be observed on the internal surface of VF 1174; see Plate V.) There is some variation in the shape of the anal notch; in the smallest specimen, VF 1177, it is V-shaped, but in the two larger examples, VF 1173 and VF 1177a, it is broader at its base and thus tends to be more U-shaped (Fig. 3). This structural difference may be due to sexual dimorphism. If so, however, it is not possible to specify which type represents the males and which the females in this species. Normally, male turtles can be distinguished from females by the characteristic depression on the posterior lobe of their plastrons, but it is not possible to determine whether or not these existed in the present sample because, in the course of fossilization, all the plastra have been somewhat depressed inward along the midline. Size alone is not a useful criterion for identifying the sexes in *Podocnemis*. In all but one of the living South American species of this genus mature females are invariably larger than males. The reverse is true, however, for *P. dumeriliana* (F. Medem, personal communication). Nor does the shape of the anal notch necessarily provide a reliable method of sex determination. Although in at least one species, *P. lewyana*, males can be identified solely on the basis of this character, there are other species (e.g., *P. vogli*) in which the two sexes appear to have similarly shaped anal notches, while in still others (e.g., *P. unifilis*) the shape of the anal notch varies considerably but evidently also randomly with respect to sex.

Pelvic scars on the plastron appear to be disposed in essentially the same positions as in the living South American species. Although partial pelves have been preserved in several of the specimens (VF 1173, 1176, 1177, and perhaps also 1177a), none of these are well enough preserved to describe in detail.

The distal half of a right humerus (VF 1059) is all that is known of the appendicular skeleton. Nothing serves to distinguish this limb fragment from comparable portions of this same bone in other species of *Podocnemis*.

Virtually no scute sulci can be detected in any of the specimens available for study. This is disappointing because their arrangement, particularly on the anterior plastral lobe, is sometimes of taxonomic significance.

DISCUSSION

Taxonomic considerations. Within the suborder Pleurodira, the presence or absence of neural bones has been accorded varying taxonomic significance. Those chelyid species that do possess neurals usually have a variable number, and in certain species of this family neurals evidently may or may not be present in different individuals of the same population. Consequently, whether or not a chelyid carapace includes some neurals, and if so, how many, has never been considered a useful taxonomic character¹. Most pelomedusid species, however, have a neural series that does not deviate from a modal number (usually 6–8) by more than one or, occasionally, two. Only two exceptions to this typical condition are known within the family, both involving extinct taxa from the Eocene of Tunisia². *Gafsachelys* (de Stefano, 1903; Bergounioux, 1952; 1955; 1956), like some chelyids, appears to have had a rather variable number of irregularly shaped neurals. *Eusarkia* (Bergounioux, 1952; 1956), described on the basis of a single specimen, has no neurals and on the basis of this and several other characters noted by Bergounioux we believe that it was probably appropriate to propose a new genus. But in no case has the absence of neurals alone been used as a taxonomic character, either at the generic or the specific level, within the Pleurodira (or among any other chelonians for that matter).

Why, then, have we described the Urumaco fossil pelomedusids as a new species of *Podocnemis*? In view of their strong overall resemblance to the living South American species of this genus it seems inappropriate to propose a new genus on the basis of a single character which, by itself, is not highly unusual nor of particularly great taxonomic significance among other members of the suborder. On the other hand, since the absence of neurals is clearly a constant character within the Venezuelan sample, this

¹ No adequate osteological descriptions of any living chelyid species have ever been published, so that reliable data are not actually available regarding the extent of intraspecific variation in the number of neurals.

² One of us (RCW) is preparing a discussion of the taxonomic status of the Tunisian fossil turtles for publication elsewhere. In this paper *Euclastochelys* (Bergounioux, 1955; 1956) is considered to be synonymous with *Gafsachelys*.

feature can hardly be regarded as an aberrant condition of no taxonomic consequence. Thus, by a process of elimination, the only alternative is to choose a procedure intermediate between regarding the lack of neurals as of enormous taxonomic importance or as of none at all and describe the Venezuelan material as a new species.

Ecological considerations. The small vertebrate fauna with which *Podocnemis venezuelensis* is associated (Royo y Gomez, 1960: 509; Pascual and Diaz de Gamero, 1969: 370 and 374) is not adequate for determining with any degree of certainty what the probable habitat of this species might have been. The mammals — a eumegamylid rodent and a toxodontid — were undoubtedly strictly terrestrial forms, while the crocodilians presumably spent most of their time in streams, lakes, or swamps. The fish — sharks, sawfish, rays, catfish, and an unidentified teleost — appear to be a mixture of marine and fresh water forms. If all these fossils were collected from a single horizon, as the scanty field evidence would suggest, then the stratum in which they occur must represent an estuarine facies. On the basis of present evidence, therefore, it is impossible to determine unequivocally whether *P. venezuelensis* was a marine or a fresh water form. To be able to do so would be particularly interesting because, while all living pelomedusids are inhabitants of fresh waters, in the past some were marine and others were fresh water forms (Wood, MS). If *P. venezuelensis* were, in fact, marine, it would be the last recorded pelomedusid so adapted.

No living species of *Podocnemis* (or any other fresh water turtle) are found in the Maracaibo basin, in which the type locality of *P. venezuelensis* lies, although they are common to the south and east of this enclave in Venezuela as well as to the west of it in Colombia. Thus, *P. venezuelensis* occurs outside the present range of the genus. Should *P. venezuelensis* eventually prove to be a fresh water rather than a marine form, its extinction may be explicable in terms of the Pleistocene climatic history of tropical South America. The Maracaibo basin is ringed by mountains except on its seaward side and hence is effectively isolated from adjacent land areas. Conceivably, a period or periods of aridity during the Pleistocene (and evidence for severe climatic fluctuations in the tropics during this epoch is accumulating — cf. Vanzolini and Williams, 1970: 94–103) may have eliminated *P.*

venezuelensis, a form presumably endemic to the basin, while the surrounding mountain barrier prevented subsequent recolonization by other species.

The fossil record of Podocnemis in South America. Few fossil species of *Podocnemis* have been described from this continent and several of these are known from such inadequate material that it is questionable whether or not they should be referred to the genus.

As previously noted, Simpson (1943) has described a partial carapace and plastron from Venezuela as *Podocnemis geologorum*¹. The single known specimen was recovered from fluvial-tile beds of Miocene age. Without a doubt, this fossil represents some kind of pleurodire because of the union of its pelvis with both carapace and plastron. Whether this specimen actually represents a pelomedusid instead of a chelyid, however, is not entirely clear. Although Simpson (1943: 57) commented "Es muy posible la existencia en esta especie de un mesoplastrón tipo *Podocnemis* de buen tamaño," the presence or absence of this pair of bones, the critical character for distinguishing members of one pleurodiran family from the other, cannot be determined. Very few potentially useful taxonomic characters can, in fact, be discerned. On the carapace, only two pleurals separate the last neural from the suprapygial. There appears to be a deep indentation in the posterior edge of the pygal at the midline, and this, together with similar but not quite so pronounced indentations in the tenth and eleventh peripherals, gives the rear margin of the carapace a serrated appearance. Whereas the last vertebral was broader than long, the two preceding ones were longer than broad. The anal notch of the plastron is rather deep and narrow, and the lateral margins of the posterior lobe are sinuous. As a consequence, the xiphiplastral tips are much more elongate than in any other taxon yet described as a pelomedusid. Simpson (1943: 61) considered the deep anal notch and serrations along the posterior border of the carapace to be the species-specific characters of *P. geologorum*, and indeed, these are quite distinctive and indicate the validity of the species. Unfortunately, however,

¹ When Simpson described the type of *P. geologorum*, it was catalogued as AMNH 6781. It now belongs to the collections of the Museo de Ciencias Naturales, Caracas, and bears the number MCN 915.

on the basis of present evidence there is no reason to believe that *P. geologorum* is really a species of *Podocnemis* or, for that matter, of any pelomedusid. It cannot yet be confidently allocated to either of the two pleurodiran families to which it must belong, the Chelyidae or the Pelomedusidae. Thus, until better material of this taxon becomes available, *P. geologorum* should be listed as *Pleurodira incertae sedis*.

Three species of *Podocnemis* — *P. harrisi* (Pacheco, 1913), *P. brasiliensis* (Staesche, 1937)¹, and *P. elegans* (Suarez, 1969) — have been described from three widely separated localities within the Baurú Formation of southern Brazil. These sediments represent terrestrial deposition, with fluvial and alluvial plain beds predominating, and are probably of late Cretaceous (Senonian) age (Oliveira, 1956: 53–54). The only specimens ever referred to *P. harrisi* were a nearly complete right xiphiplastron and several peripherals (Pacheco, 1913: 37, pl. 3 [figs. 6a–e], pl. 4 [fig. 6]). Ischial and pubic scars on the visceral surface of the xiphiplastron clearly indicate that some kind of pleurodire is represented, but no other taxonomically useful evidence exists. It is therefore impossible to determine whether *P. harrisi* is a chelyid or a pelomedusid. Reference of this species to *Podocnemis* was unjustifiable, as Schmidt noted long ago (1931: 253). Furthermore, since the type material is now apparently lost (Price, 1953: 10), "*P. harrisi*" must be regarded as a *nomen vanum*.

On the basis of some photographs of a partial plastron, a carapace fragment², and three associated pleurals, Staesche (1937) described *P. brasiliensis*. The xiphiplastra of this species do not appear to differ in any appreciable way from those of *P. harrisi*, and therefore Simpson (1943: 61) may well have been correct in suggesting that *P. brasiliensis* is a synonym of *P. harrisi*, although Staesche (1937: 302–303) noted that his material differed in that it represented a somewhat larger individual with a different kind of sculpturing on the external surface of the shell, factors which might or might not be of taxonomic significance.

¹Staesche (1944) is merely a translation of Staesche (1937) from German into Portuguese.

²This carapace fragment, together with a previously undescribed anterior lobe of a plastron from the same locality, was subsequently referred to a new genus and species, *Roxochelys wanderleyi*, by Price (1953).

Small, laterally placed mesoplastra were present, even though no longer preserved, so that *P. brasiliensis* is clearly a pelomedusid. An appropriate generic determination cannot at present be made, however, because much of the anterior plastral lobe, so critical for pelomedusid shell taxonomy, is missing. Thus, the specimen can neither be certainly referred to *Podocnemis* nor, owing to its imperfect preservation, can any species-specific characters be established. Until better material is available, therefore, the plastron and pleurals to which the name *P. brasiliensis* now applies should be designated as Pelomedusidae gen. et sp. indet. ("*Podocnemis brasiliensis*" Staesche).

Unlike the other two dubious "species" of *Podocnemis* from the Baurú Formation, *P. elegans* is clearly valid and referable to this genus. It is the only South American fossil pelomedusid yet described for which associated shells and skulls have been recovered. Furthermore, it is the oldest representative of *Podocnemis* known anywhere. It was described on the basis of two specimens, an essentially complete shell and a well-preserved skull belonging to a different individual¹. A detailed description of this species will not be presented here since an account, based on additional new material as well as the original hypodigm, is being prepared by one of us (RCW) for separate publication. Some of the salient characters may be briefly noted, however. In most respects the shell is typical of all South American species of *Podocnemis*, but the shapes of the first two neurals are unique: instead of being spindle-shaped, the first is hexagonal, with the postero-lateral sides much shorter than the antero-lateral ones; and the second, rather than being hexagonal, is subrectangular. A unique feature of the skull is the total absence of triturating ridges on the palatal surface of the upper jaw. All other species have from one to three triturating ridges, the exact number being characteristic of different species. In addition, there does not seem to be an antero-posterior

¹ Suarez (1969: 37) stated: "Designamos como tipo da nova especie a carapaca e plastrão com craneo e diversos elementos esqueléticos . . ." The shell and skeletal elements belong to one individual and there is in fact a badly crushed skull (which was not illustrated or discussed) associated with them, but it is not the skull described by Suarez. This is an isolated one from a much larger individual. Both specimens are in the paleontological collections of the Faculdade de Filosofia, Ciências e Letras de Presidente Prudente; they bear no catalog numbers.

forehead groove between the orbits. Of the other South American species of *Podocnemis*, only *P. dumeriliana* lacks this groove. Perhaps the most extraordinary aspect of the skull of *P. elegans* is its modern appearance; archaic or ancestral features that one might expect to find in such an ancient species are notably lacking.

Cattoi and Freiberg (1958) described *Podocnemis argentinensis* from the Santa Barbara Formation¹ in the Province of Jujuy, Argentina. It is known from a large part of a plastron, lacking the terminal portions of the anterior and posterior lobes as well as much of the bridges, and most of the right epiplastron of a second individual. The systematic position of this form is uncertain. Laterally placed mesoplastra were definitely present, as evidenced by the semicircular excavations on either side of the plastron at the base of the bridge, so that *argentinensis* clearly represents some kind of pelomedusid. Too little of the shell has been preserved, however, to permit assignment to *Podocnemis* with any degree of confidence. At a lower taxonomic level, the characters used to define the species are in some cases questionable and in others of little or no taxonomic significance. Cattoi and Freiberg described the entoplastron as cordiform, but in their figure and plate it appears to be quadrangular. Examination of the specimen itself indicates that the entoplastron is slightly damaged anteriorly and that it was probably diamond-shaped originally. Small, triangular gular scutes are characteristic of most pelomedusids, but the relatively small intergular, which was probably pentagonal, is certainly reminiscent of the condition typical of South American species of *Podocnemis* and the North American *Bothremys* (Gaffney and Zangerl, 1968). The various scute proportions cited by Cattoi and Freiberg in their diagnosis yield no useful taxonomic information. Anastomosing vermiculations cover the external plastral surface as in the majority of pelomedusid

¹Various ages have been assigned to this stratigraphic unit, formerly referred to as the Margas Multicolores. Cattoi and Freiberg placed it in the late Cretaceous, while Bardack (1961) considered it to be middle Tertiary. The recent discovery of a mammal skull high in the formation indicates a Paleocene or early Eocene age (R. Pascual, personal communication). There is some uncertainty as to whether these beds are of marine or terrestrial origin (Cattoi and Freiberg, 1958: 59).

genera¹. Until better material becomes available, it will not be possible to determine the systematic position of this turtle. In the meantime, it must be referred to as *Pelomedusidae* gen. et sp. indet. ("*Podocnemis argentinensis*" Cattoi and Freiberg).

The type and only specimen of *Podocnemis bassleri* (Williams, 1956) is a large, exceedingly well-preserved skull. It was collected in eastern Peru from beds of the Contamana Group, which includes sediments believed to range in age from Eocene to possibly at late as Pliocene. Williams, on the basis of information supplied by Kummel, reported that the skull "came from the uppermost part of the . . . group," which suggests that its age falls within the latter part of the Tertiary. He further remarked that "The fossil itself is so close to a Recent species as to tend to support the latest date geologically permissible." The skull differs only in minor details from that of the living *P. expansa*. It seems fairly certain that *P. bassleri* was closely related, if not directly ancestral, to this species.

Unfortunately, the evolutionary history of *Podocnemis* in South America cannot be reconstructed on the basis of present information. Only three fossil species — *P. bassleri*, *P. elegans*, and *P. venezuelensis* — are of unquestionable validity. One of these, *P. bassleri*, is clearly very closely related to *P. expansa*. The relationships of the other two extinct species to living South American forms are uncertain, owing to their distinctive shell characters. With the exception of *P. lewyand*², the living South American species of *Podocnemis* are all strikingly similar in terms of shell

¹ Cattoi and Freiberg's figure 1 shows the entoplastron as being nearly encompassed by unusually large epiplastra, a condition unknown in any other chelonians that we are aware of. However, their sketch does not accurately represent the positions of the sutures between the epiplastra and hyoplastra; these are, in fact, disposed in typical pelomedusid fashion, extending outward from the lateral apices of the entoplastron.

² Through the courtesy of Professor F. Medem, one of us (RCW) has been able to examine a series of six *P. lewyana* shells in the collections of the Instituto Roberto Franco at Villavicencio, Colombia. None of these has a suprapygal bone on the carapace; instead, each of the last (eighth) pleurals is subtriangular, not trapezoidal as is the case in other species of the genus, and these pleurals are in continuous contact along the midline from the posterior end of the seventh pair of pleurals to the pygal.

morphology. Only small structural details characteristic of each taxon permit differentiation among them on the basis of shells alone. *P. venezuelensis* stands markedly apart from all other species of the genus in its total lack of neurals, and certainly could not have given rise to any of the living forms. Nothing remotely resembling the shapes of the first two neurals in *P. elegans* is encountered elsewhere in the genus. So conservative in structure is this part of the shell in all other species (except, of course, for *P. venezuelensis*), and so radically different is it in *P. elegans*, that this species could hardly have been ancestral to any or all of the later species known from South America. Thus, neither *P. elegans* nor *P. venezuelensis* has any obvious relationship to living species of the genus or to each other. A much better fossil record for *Podocnemis* will be necessary before a meaningful picture of its evolutionary history in South America can be formulated.

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We are particularly grateful to Señora Frances Charlton de Rivero, retired professor of paleontology at the Escuela de Geología y Minas in Caracas, not only for her gracious hospitality but also for having provided laboratory facilities while the material here described was being studied. Both authors have examined the type specimen of "*Podocnemis*" *geologorum* and one of us (RCW) has also been able to examine the types of "*P. argentinensis*," *P. bassleri*, and "*P. brasiliensis*." We would like to thank the curators of the various institutions at which these fossils are housed for permission to study them. Through the kindness of Professor José Martín Suárez, RCW has not only been able to study the type material of *P. elegans* but also to visit the locality from which it was recovered. Without a generous grant to RCW from the National Geographic Society, none of this work would have been possible. We are much obliged to Professors F. Medem, B. Patterson, P. E. Vanzolini, and E. E. Williams, and to Dr. M. Freiberg for their comments and discussions on various aspects of this manuscript.

LITERATURE CITED

- BARDACK, D. 1961. New Tertiary teleosts from Argentina. *American Mus. Novitates*, No. 2041: 1-27.
- BERGOUNIOUX, F. M. 1952. Les chéloniens fossiles de Gafsa. Appendix to: Arambourg, C., and J. Signeux. Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). Notes et Mémoires No. 92, Service Géologique de Maroc: 377-396, pls. 45-46.
- . 1955. La famille des Eusarkiids. *Comptes Rendus de l'Acad. Sci.*, **240**: 1455-1457.
- . 1956. Les reptiles fossiles des dépôts phosphatés sud tunisiens. *Annales des Mines et de la Géologie (Tunis)*, No. 15: 1-105, pls. 1-17.
- CATTOI, N., AND M. A. FREIBERG. 1958. Una nueva especie de "*Podocnemis*" del cretáceo argentino. *Physis*, **21**(60): 58-67.
- DACQUÉ, E. 1912. Die fossilen Schildkröten Aegyptens. *Geol. Paläont. Abhandl., N. F.*, **10**(4): 275-337, pls. 36-37.
- GAFFNEY, E. S., AND R. ZANGERL. 1968. A revision of the chelonian genus *Bothremys* (Pleurodira, Pelomedusidae). *Fieldiana. Geol.*, **16**(7): 193-239.
- OLIVEIRA, A. I. DE. 1956. Brazil. In W. F. Jenks (ed.), *Handbook of South American Geology*. *Geol. Soc. Amer. Mem.* **65**: 1-378.
- PACHECO, J. A. 1913. Notas sobre a geologia do valle do Rio Grande, a partir da fóz do Rio Pardo até a sua confluencia com o Rio Paranahyba. In J. dos Dourados (ed.), *Exploração do Rio Grande e de seus afluentes*. *Comissão Geographica e Geologica do Estado de São Paulo*: 33-38.
- PASCUAL, R., AND M. L. DIAZ DE GAMERO. 1969. Sobre la presencia del genero *Eumegamys* (Rodentia, Caviomorpha) en la formación Urumaco del Estado Falcón (Venezuela). Su signification cronologica. *Bol. Informativo, Assoc. Venezolana de Geol., Min. Pet.*, **12**(10): 369-387.
- PRICE, L. I. 1953. Os quelônios de formação Baurú. Cretáceo terrestre do Brasil meridional. *Dept. Nac. Prod. Min., Div. Geol. Min., Bol.* **147**: 1-34.
- ROYO Y GOMEZ, J. 1960. Los vertebrados de la formacion Urumaco, estado Falcón. *Mem. III Congr. Geol. Venezolano*, **2**: 506-510.
- SCHMIDT, K. P. 1931. A fossil turtle from Peru. *Field Mus. Nat. Hist. Publ.* **299**, *Geol. Ser.*, **4**(8): 251-254.
- . 1940. A new turtle of the genus *Podocnemis* from the Cretaceous of Arkansas. *Geol. Ser. Field Mus. Nat. Hist.*, **8**(1): 1-12.

- SILL, W. D. 1970. Nota preliminar sobre un nuevo gavial del Plioceno de Venezuela y una discusión de los gaviales sudamericanos. *Ameghiniana*, **7**(2): 151-159.
- SIMPSON, G. G. 1943. Una tortuga del Terciario de Venezuela. *Rev. Ministerio de Fomento, Caracas, Venezuela*, año 5, nos. 51-52, April - Sept. 1943: 53-64.
- STAESCHE, K. 1937. *Podocnemis brasiliensis* n. sp. aus der Oberen Kreide Brasiliens. *Neues Jahrb. Min., Geol. Paläont.*, **77**: 291-309.
- . 1944. Uma tartaruga do cretaceo superior do Brasil. *Dep. Nac. Prod. Min., Div. Geol. Min., Bol.* **114**: 1-24, pls. 16-20.
- STEFANO, G. DE. 1903. Nuovi rettili degli strati a fosfato della Tunisia. *Bol. Soc. Geol. Ital.*, **22**: 51-80.
- SUAREZ, J. M. 1969. Um quelônio da formação Bauru. *Dept. Geografia, Fac. de Filos., Cien. Letras Pres. Prudente*, No. 2: 35-54.
- SWINTON, W. E. 1928. Note on the fossil reptilia collected by Mr. Donald Stewart in Venezuela. *Quart. Jour. Geol. Soc.*, **84**, Pt. 3: 583.
- VAN FRANK, R. 1957. A fossil collection from northern Venezuela. 1. *Toxodontidae* (Mammalia, Notoungulata). *American Mus. Novitates*, No. 1850: 1-38.
- VANZOLINI, P. E., AND E. E. WILLIAMS. 1970. South American anoles: the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). *Arq. Zool., S. Paulo*, **19**(1-2): 1-124.
- WILLIAMS, E. E. 1956. *Podocnemis bassleri*, a new species of pelomedusid turtle from the late Tertiary of Peru. *American Mus. Novitates*, No. 1782: 1-10.
- ZANGERL, R. 1948. The vertebrate fauna of the Selma Formation of Alabama. part II. The pleurodiran turtles. *Fieldiana: Geol. Mem.* **3**(2): 19-56.

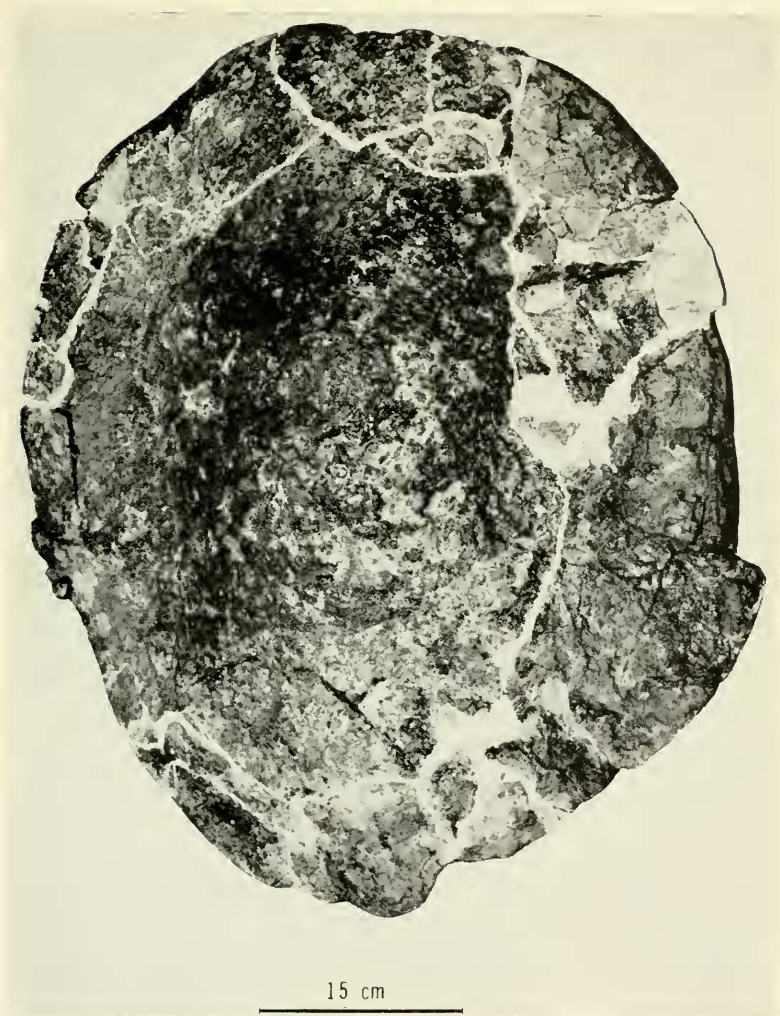


Plate I. Dorsal view of the type carapace (VF 1176) of *Podocnemis venezuelensis*.

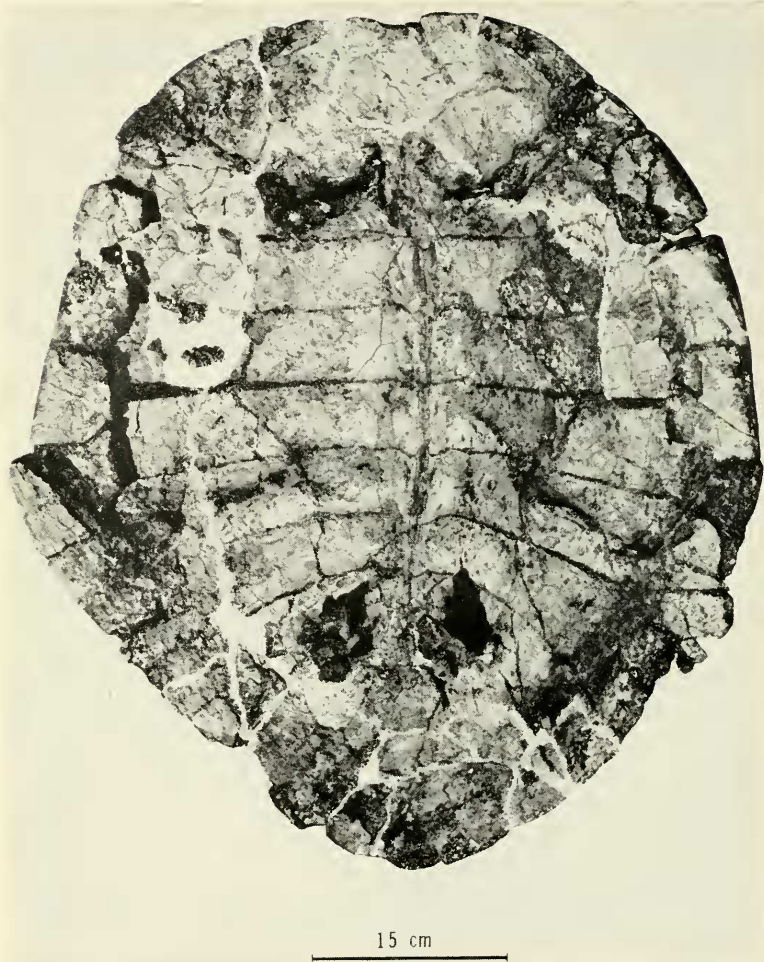


Plate II. View of the visceral surface of the type carapace (VF 1176) of *Podocnemis venezuelensis*. Note the absence of neural bones.



Plate III. View of the visceral surface of the type plastron of *Podocnemis venezuelensis* (VF 1173), showing the disposition of the pelvic attachments to it.

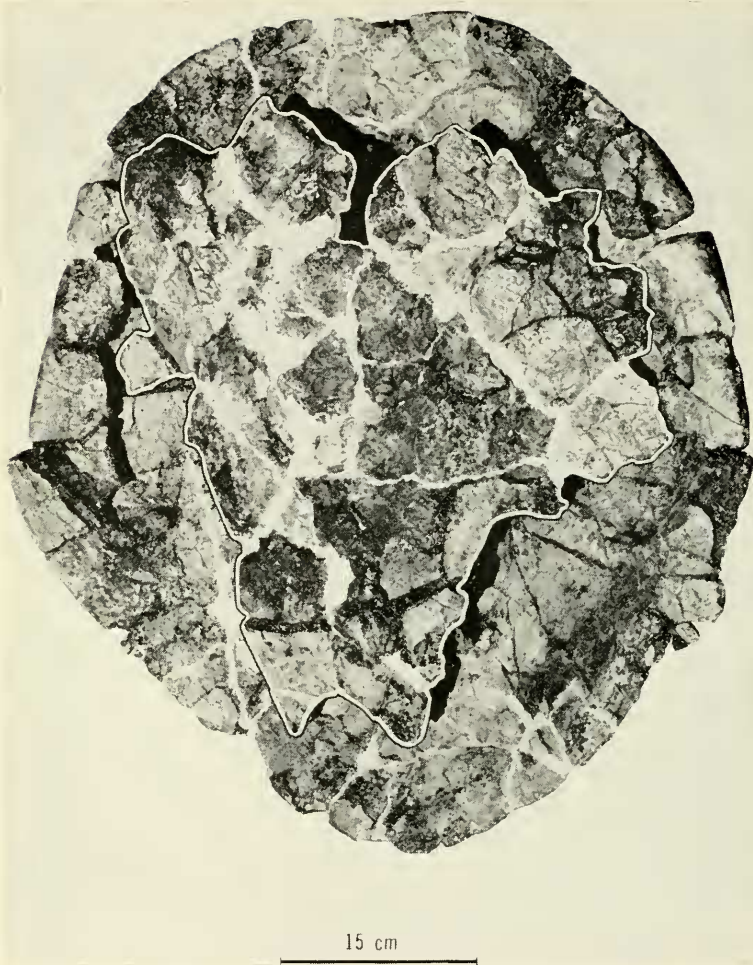


Plate IV. Ventral view of the type shell of *Podocnemis venezuelensis*, with the plastron (VF 1173) positioned correctly in relation to the carapace (VF 1176).

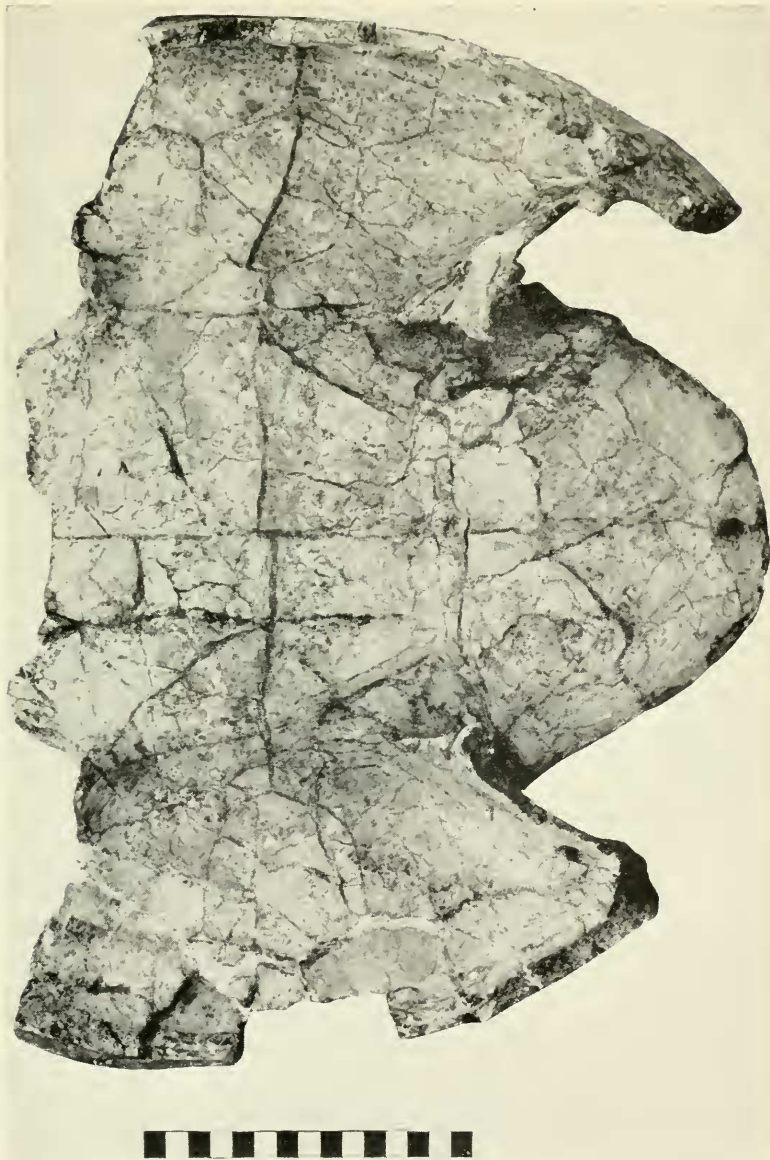


Plate V. The visceral surface of VF 1174, a partial plastron of *Podocnemis venezuelensis*, showing clearly the outlines of the laterally placed mesoplastra.